TEMPORAL VARIATION IN MICROHABITAT RELATIONSHIPS AMONG GREBES AND COOTS

GREGORY G. BARNES[1] AND THOMAS D. NUDDS[1]

ABSTRACT.—Interspecific competition may shape species' niches such that relative niche positions remain consistent in niche space. However, during times when competition is relaxed, it has been hypothesized that significant rearrangement of species' niches occurs, both relative to each other and to available niche space. We compared microhabitat niche relationships among coexisting Horned Grebes (*Podiceps auritus*), Pied-billed Grebes (*Podilymbus podiceps*), and American Coots (*Fulica americana*) in aspen parkland near Minnedosa, Manitoba, from 1982 to 1984. Despite annual variation in the structure and abundance of microhabitats due to fluctuating water levels, niche relationships among grebes and coots remained relatively consistent. Coots generally occupied shallow sites with tall vegetation, and Horned Grebes used deep sites with little vegetation; both species used sites with little spatial complexity. Pied-billed Grebes occupied sites intermediate to those of the other species with respect to water depth and vegetation height, and used more spatially heterogeneous sites. In two low water years, overall niche separation was greatest along a depth-vegetation height dimension. In a high water year, niche separation was greatest along a spatial complexity dimension. Nevertheless, relative amounts of niche separation remained consistent; coots and Horned Grebes were always most different, and coots and Pied-billed Grebes were always most similar, in microhabitat use. These data support the idea that niche organization in this guild results from interspecific interactions rather than random processes. *Received 23 Jan. 1989, accepted 20 May 1989.*

Until the mid-1970s, interspecific competition was thought to be responsible principally for observed niche sizes, niche overlap, and relative abundances of species in ecological communities (e.g., Cody and Diamond 1975). Wiens (1977), however, thought that fluctuations in resource abundance, especially for vertebrates, should cause interspecific competition to be only periodically important as a factor influencing community structure. His "variable environments" hypothesis contended that populations of coexisting species in variable environments might compete only rarely during ecological "crunches."

The next decade witnessed vigorous debate about the importance of competition and the adequacy of the evidence for it (e.g., Strong et al. 1984). By the mid-1980s, the debate moderated (e.g., Diamond and Case 1986) coincident with the emergence of a "paradigm of scale" (Allen and Starr 1982). Accordingly, the variable environments hypothesis was recast as a specific example of the way that scale affects patterns in data and interpretations about the factors producing the patterns (e.g., Wiens 1986).

---

[1] Dept. of Zoology, Univ. of Guelph, Guelph, Ontario N1G 2W1 Canada.

For example, "snapshot" assessments of niche sizes, shapes and positions, and other attributes of communities of songbirds can produce very different results from one year to the next in variable shrubsteppe habitats (Wiens 1981; Wiens and Rotenberry 1979, 1980) and deciduous forests (Holmes et al. 1986). Wiens (1981) argued that this type of evidence was inconsistent with the classical view that competition both shapes species' niches and causes species to maintain relatively static positions in niche space.

Nudds (1982) described interspecific niche relationships among Horned Grebes (*Podiceps auritus*), Pied-billed Grebes (*Podilymbus podiceps*), and American Coots (*Fulica americana*) coexisting on small wetlands in a single year. Here, we report on subsequent years of observations of microhabitat niche relationships among the same species at the same site over a period when resource abundance fluctuated. We tested whether interspecific niche relationships varied among years or whether species maintained static positions in niche space relative to each other and to available niche space.

STUDY AREA AND METHODS

Data were collected from mid-April to early July, 1982 to 1984, on a 1.62 km² study area in aspen parkland approximately 10 km NE of Minnedosa, Manitoba (50°N, 99°W). The region periodically experiences drought; both water levels within wetlands and the number of wetland basins containing water vary from year to year. Six of the nine potholes on the study area were present in all three years and were used for this study. They included temporary (Type 1; Smith 1971), semipermanent (Type 3), and permanent (Type 5) wetlands. Complete descriptions of the area can be found in Nudds (1982).

The perimeters of each pothole were marked at 10-m intervals with wooden stakes and several microhabitat characteristics were measured at each grid point (see Nudds 1982). Water depth was measured to the nearest 1.0 cm in late April and mid-May of each year. Average depth for a quadrat was obtained from measurements at the four grid points which delineated it. Structural aspects of the emergent vegetation were measured using a profile board (see Nudds 1977) at each grid point. Vegetation density in each of four strata (0.25, 0.5, 1.0, 1.5 m above the water surface) was estimated as percent of the profile board occluded by vegetation. Proportions (p) of the total amount of vegetation were summed over the four strata (i), and substituted into $1/\Sigma p_i^2$, which is an index of the complexity of vertical microhabitat structure. Vegetation height was measured to the nearest 1.0 cm with a stick fastened to the profile board. The value of each variable for a quadrat was then calculated as the mean of the values for the four grid points delineating it. Also, the number of "islands" of emergent vegetation in each of three size categories (<0.3 m, >0.3 m but <1 m, and >1 m diameter) in each quadrat were counted. Island-size diversity was calculated from $1/\Sigma p_i^2$, where p is the porportion of all "islands" in the ith size category. In total, 20 structural attributes were used to describe microhabitats (see Table 1).

For purposes of comparing changes in water levels among years, mean maximum water depth for each pothole was obtained by averaging the depths of the four deepest quadrats.

Microhabitat use by *F. americana*, *P. auritus* and *P. podiceps* was observed from blinds entered before sunrise from mid-April to early July each year. Observations were made on

TABLE 1

Factor Loadings and Amount of Variance Accounted for by PCA on Microhabitat Variables during 1982–1984

Variable	Description of variables	1982 PC1	1982 PC2	1983 PC1	1983 PC2	1984 PC1	1984 PC2
Depth	Water depth	−0.70	−0.15	−0.39	−0.56	−0.86	0.17
L1	Vegetation density in each of 4 layers	0.90	−0.31	0.96	−0.10	0.92	0.16
L2		0.77	−0.37	0.88	−0.29	0.79	0.58
L3		0.27	0.03	0.40	−0.16	0.41	0.76
L4		0.13	−0.01	0.29	−0.11	0.27	0.57
SumL	Total vegetation density	0.66	−0.38	0.97	−0.17	0.87	0.45
P1	Proportion of vegetation at each layer	0.82	−0.18	0.92	−0.01	0.87	−0.24
P2		0.23	−0.29	0.39	−0.38	0.35	0.68
P3		−0.69	0.25	−0.95	0.12	−0.77	0.28
P4		−0.84	0.31	−0.96	0.13	−0.93	−0.20
Vegdiv	Vertical complexity of vegetation	−0.69	−0.21	−0.92	0.12	−0.58	0.10
Height	Vegetation height	0.87	0.64	0.90	0.05	0.75	0.23
N1	Number of "islands" in each of 3 size categories	0.42	0.53	0.23	0.74	0.65	−0.46
N2		0.67	0.06	0.14	0.77	0.74	−0.34
N3		0.56	0.55	0.50	0.32	0.70	−0.10
SumN	Number of "islands"	0.76	0.64	0.33	0.81	0.77	−0.42
NP1	Proportion of "islands" in each size category	0.46	0.35	0.09	0.67	0.69	−0.34
NP2		0.54	−0.26	−0.07	0.52	0.60	−0.20
NP3		0.35	0.44	0.48	−0.30	0.39	0.06
Isldiv	"Island size" diversity	0.75		0.39	0.73	0.85	−0.18
λ_i	Percent of variance explained	49.7	16.8	41.6	19.6	51.1	14.5

61, 74, and 59 days in 1982, 1983, and 1984, respectively, using spotting scopes and binoculars. The locations of individual coots and grebes were recorded on scale maps of each pothole at 0.5-h intervals for 4 h. Values for microhabitat characteristics for the quadrat in which an individual was recorded were assigned to that individual.

Stepwise discriminant function analysis (DFA, Nie et al. 1983), preceded by principal components analysis (PCA, Nie et al. 1983), was used to delineate species' differences in microhabitat use and to assign relative importance to those structural habitat features that segregated species. Species' scores on the PCs were used as orthogonal discriminating variables in DFA (Green 1979). Between-year variation in structural characteristics of microhabitat dimensions was quantified by comparing the variable loadings on the same PCs produced from separate analyses of data from different years (Rotenberry and Wiens 1980: 1242–1243, Landres and MacMahon 1983:186, Mulhern et al. 1985:475–476) using Kendall's ranked order correlations (Sokal and Rohlf 1969). If the ranked-order correlations were significant, we deemed the structure of the axes sufficiently similar for purposes of interannual comparisons of species' distributions along them. If they were uncorrelated, then inspection of the variable loadings would reveal how components of wetland structure varied interannually relative to one another. Finally, we examined between-year variation in species' pairwise niche separation (that is, the pairwise F-statistics, or among-to-within species variances in discriminant space [Nie et al. 1983]) and between year variation in mean niche position to see whether fluctuations in water levels across years affected niche relationships among grebes and coots.

RESULTS AND DISCUSSION

The numbers of observations of coots, Horned Grebes, and Pied-billed Grebes, respectively, in each year were: 1982: 205, 160, and 25: 1983: 624, 154, and 67; and 1984: 641, 59, and 124. Two microhabitat dimensions were identified by PCA each year and together accounted for 67%, 62%, and 66% of the total variance among the original microhabitat variables in 1982, 1983, and 1984, respectively (Table 1). In five of six between-year comparisons, the factor loadings for the microhabitat variables on the first and second principal components were significantly correlated (Table 2). In each year, PC1 described a continuum of microhabitat structure ranging from tall dense, spatially uniform stands of emergent vegetation in shallow water to deep, open water sites with no emergent vegetation (Table 1). Similar patterns of microhabitat structure were also evident in 1978 (Nudds 1982).

Correlations involving loadings from 1983, however, were lower than the correlation between loadings in 1982 and 1984 (Table 2). Increased water levels substantially altered habitat structure in 1983 (Fig. 1). Potholes in 1983 were characterized by a shallow, flooded perimeter of open water around stands of emergent vegetation which, in turn, surrounded deep, but also open, water in the centers of wetlands (Fig. 1). Thus, vegetation that was tall, dense, and in shallow water in 1982 and 1984 occurred at intermediate water depths in 1983, so the variable loadings

TABLE 2

KENDALL'S RANK CORRELATION COEFFICIENTS[a] BETWEEN VARIABLE LOADINGS ON
PRINCIPAL COMPONENTS DESCRIBING MICROHABITATS USED BY GREBES AND COOTS IN
1982–1984

Component scores correlated	Principal component 1	Principal component 2
1982 vs 1983	0.58	0.66
1983 vs 1984	0.64	−0.62
1982 vs 1984	0.85	−0.43, NS

[a] Significant at the 5% confidence level ($P < 0.037$) adjusted for effects of non-independence among the 3 pairwise correlations for each principal component.

on PC1 in 1983 were not as tightly correlated with those of either 1982 or 1984 (Table 2).

Variables loaded differently onto PC2 in 1984 compared with 1982 and 1983. In all years, PC2 described a gradient in microhabitat complexity from uniform stands of emergent vegetation to more structurally complex stands highly interspersed by water (Table 1). In 1984, however, 16 of 20 variable loadings on PC2 changed sign compared with the same loadings in 1982 and 1983 (Table 1), and rank correlations between factor loadings in 1984 compared with 1982 and 1983 were negative (Table 2). We interpret this to mean that in 1984, PC2, relative to PC1, was rotated roughly in a direction opposite to that in 1982 and 1983. Thus, despite yearly differences in water levels that produced small differences in habitat structure described by PC1, PC2 described the same aspects of habitat structure in each year.

In all years, DFA identified both principal dimensions as important ecological segregators of species, although the relative importance of each dimension was not consistent among years (Table 3). In 1982 and 1984, overall microhabitat separation among species was greatest along the depth dimension (Table 3). Though microhabitat niche separation remained markedly high, it decreased after PC2 entered the discriminant model in both years (Table 3), reflecting the greater degree of species' separation along the depth gradient than along the spatial complexity dimension. In both years, species' pairwise niche separation was greatest between *F. americana* and *P. auritus* and less between *F. americana* and *P. podiceps,* and *P. podiceps* and *P. auritus* (Fig. 2).

In 1982 and 1984, shallow sites with tall vegetation were used by *F. americana, P. auritus* used deep sites with short vegetation, and *P. podiceps* was found at intermediate water depths and occurred in more patchy microhabitats than the other species (Fig. 2).
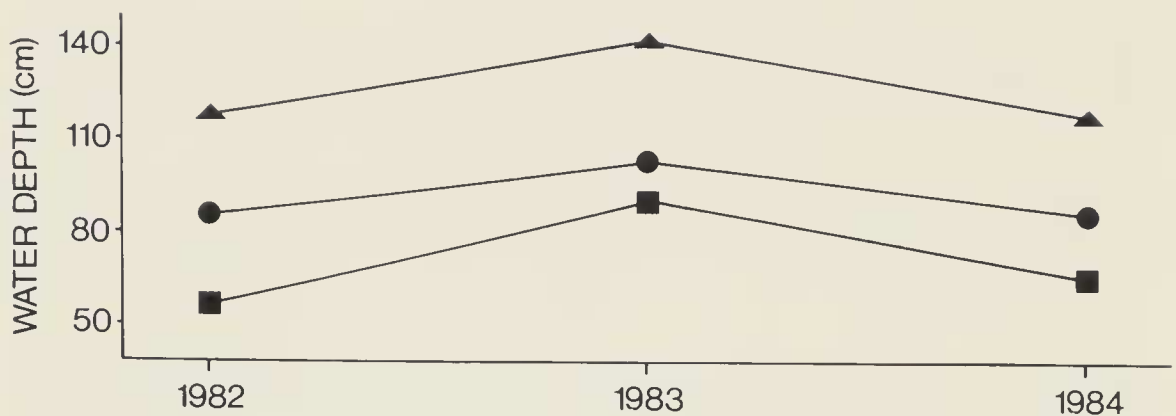
FIG. 1.   (Upper) Mean maximum water depths of deep (▲), intermediate (●), and shallow (■) potholes used by grebes and coots from 1982–1984. (Lower) An illustration of wetland conditions from (left to right) 1982–1984 in a typical pothole. Note the flooded perimeter and ring of emergent vegetation in the wetland in 1983 (middle) compared with the other years.

In 1983, unlike 1982 and 1984, species segregated most along the spatial complexity dimension (Table 3). Again, the inclusion of the other micro-habitat dimension (in this case, the depth gradient PC1) caused overall species' separation to decrease, although species still differed markedly in microhabitat use (Table 3). Also unlike 1982 and 1984, *F. americana* and *P. auritus* used sites very similar in vegetation height (PC1); but like 1982 and 1984, *P. podiceps* used patchier microhabitats than the other species. Like 1982 and 1984, niche separation was greatest for *F. americana-P. auritus* and less for the others (Fig. 2).

Nudds (1982) concluded that it was not necessary to invoke interference competition as an explanation for observed differences in microhabitat use among grebes and coots (Faaborg 1976). However, he could not re-solve whether any other form of competition was responsible for the observed differences among species, because his was a "snap-shot" of differences in microhabitat use among species during a single season. Our study, however, identified patterns of microhabitat niche separation and position over three years that were similar to each other and similar to
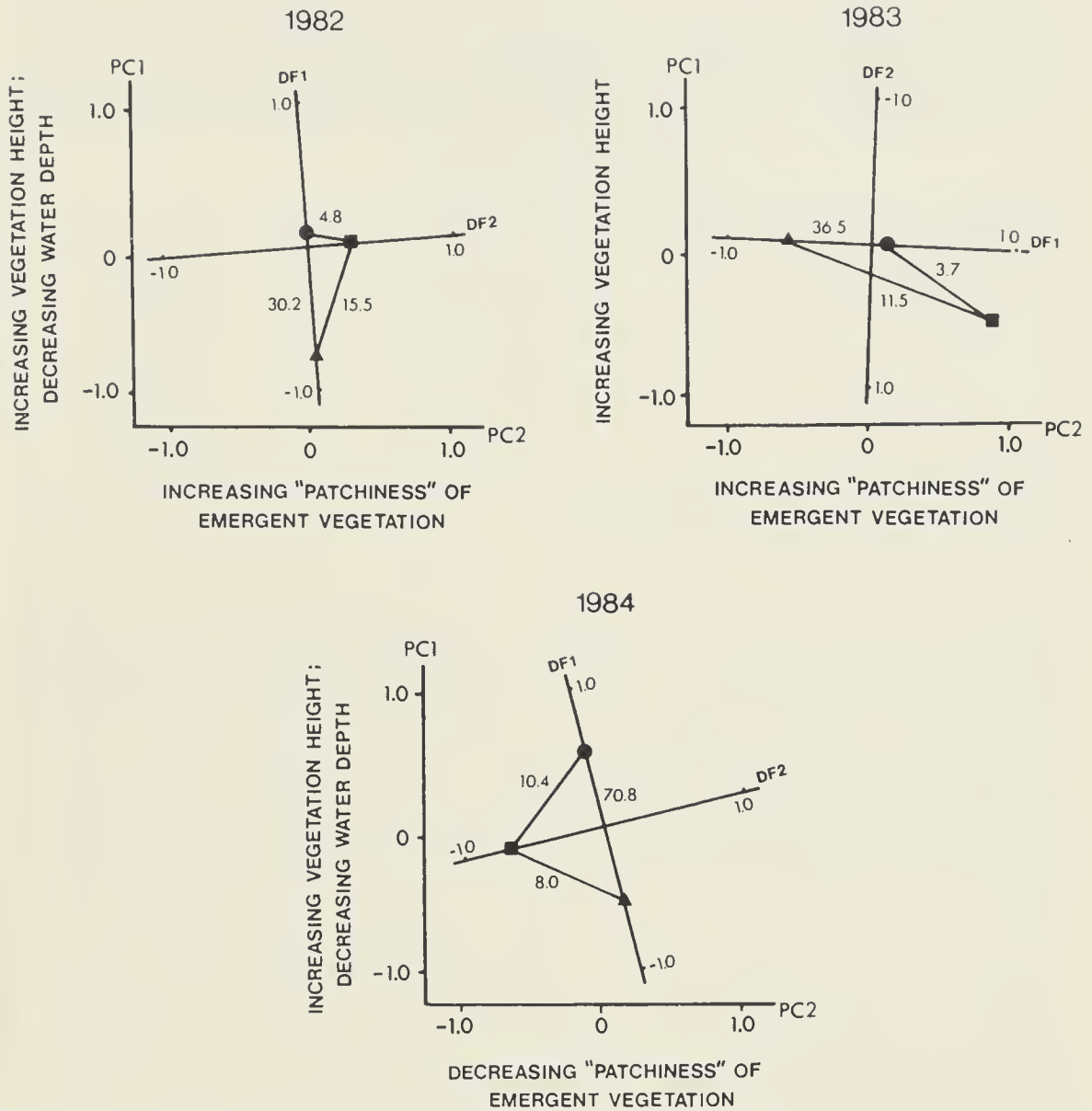
FIG. 2. Temporal variation in the microhabitat relationships among Horned Grebes (▲), Pied-billed Grebes (■), and American Coots (●) in two-dimensional space, and the discriminant axes along which species segregated. Numbers adjacent to lines connecting species' centroids are maximum ratios of among-to-within species variances in microhabitat use from discriminant analysis.

those found earlier (Nudds 1982). Thus, patterns of microhabitat use appear relatively robust to fluctuations in microhabitat abundance and distribution. The positions of species' niches, both relative to each other and relative to available niche space, were altered little despite that variation. This finding is consistent with the idea that microhabitat use by these species is determined more by biological interactions than it is by random assembly.

TABLE 3

OVERALL MICROHABITAT SEPARATION[a] IN DISCRIMINANT SPACE AFTER ENTERING THE FIRST
AND SECOND PRINCIPAL COMPONENTS FOR THE GREBE-COOT GUILD AT MINNEDOSA,
MANITOBA DURING 1982–1984

Year	Principal component[b]	F-value	P-value
1982	1	30.16	0.0001
	2	4.75	0.009
1983	2	43.84	0.0001
	1	30.19	0.0001
1984	1	70.54	0.0001
	2	35.75	0.0001

[a] Among-to-within species variance in discriminant space.
[b] Order selected for entry into the discriminant analysis.

Environments vary with varying amplitudes and periodicities. Further,
attributes of communities of species with differing life-history traits might
be expected to differ in response to variations in environmental condi-
tions, that is, to differ in "tracking ability" (Roughgarden 1979:398, Boyce
and Daley 1980). Wiens (1977) suggested that competition should be a
temporally sporadic, often ineffective, interaction in variable environ-
ments and found little evidence that communities of shrubsteppe birds
track fluctuating resources (Wiens 1986). Conversely, Cody (1981) thought
that communities might track resource fluctuations and remain in a dy-
namic but resource-limited state. Nudds (1983), for example, thought that
competition played a role in structuring waterfowl communities in vari-
able environments. He suggested that over the long term, ducks tended
to equilibrate population sizes with available resource levels because high
fecundities and long life spans enable ducks to track fluctuations in re-
source abundance. Our results suggest that grebes and coots might respond
to environmental variability more like ducks than shrubsteppe birds.
Although grebes and coots live in variable environments, they neverthe-
less show relatively consistent niche relationships from year to year. Per-
haps Wiens' (1977) "variable-environments" hypothesis is less appro-
priate for waterfowl, such as grebes and coots, if they can better track
resource fluctuations than can short-lived shrubsteppe birds.

LITERATURE CITED

ALLEN, T. H. F. AND T. D. STARR. 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago, Illinois.

BOYCE, M. S. AND D. J. DALEY. 1980. Population tracking of fluctuating environments and natural selection for tracking ability. Am. Nat. 115:480–491.

CODY, M. L. 1981. Habitat selection in birds: the roles of vegetation structure, competitors and productivity. BioScience 31:107–113.

——— and J. M. DIAMOND [eds.]. 1975. Ecology and evolution of communities. Harvard Univ. Press, Cambridge, Massachusetts.

DIAMOND, J. AND T. J. CASE [eds.]. 1986. Community ecology. Harper and Row, New York, New York.

FAABORG, J. 1976. Habitat selection and territorial behavior of the small grebes of North Dakota. Wilson Bull. 88:390–399.

GREEN, R. H. 1979. Sampling design and statistical methods for environmental biologists. Wiley, New York, New York.

HOLMES, J. T., T. W. SHERRY, AND F. W. STURGES. 1986. Bird community dynamics in a temperate deciduous forest: long-term trends at Hubbard Brook. Ecol. Monogr. 56: 201–220.

LANDRES, P. B. AND J. A. MACMAHON. 1983. Community organization of arboreal birds in some oak woodlands of western North America. Ecol. Monogr. 53:183–208.

MULHERN, J. H., T. D. NUDDS, AND B. R. NEAL. 1985. Wetland selection by Mallards and Blue-winged Teal. Wilson Bull. 97:473–485.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT. 1983. SPSSX Users Guide. McGraw-Hill, Chicago, Illinois.

NUDDS, T. D. 1977. Quantifying the vegetative structure of wildlife cover. Wildl. Soc. Bull. 5:113–117.

———. 1982. Ecological separation of grebes and coots: interference competition or microhabitat selection? Wilson Bull. 94:505–514.

———. 1983. Niche dynamics and organization of waterfowl guilds in variable environments. Ecology 64:319–330.

ROTENBERRY, J. T. AND J. A. WIENS. 1980. Habitat structure, patchiness and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61: 1228–1250.

ROUGHGARDEN, J. 1979. Theory of population genetics and evolutionary ecology: an introduction. MacMillan, New York, New York.

SMITH, A. G. 1971. Ecological factors affecting waterfowl production in the Alberta parklands. U.S.F.W.S. Res. Publ. 98.

SOKAL, R. R. AND F. J. ROHLF. 1969. Biometry. Freeman, San Francisco, California.

STRONG, D. R., D. SIMBERLOFF, L. G. ABELE, AND A. B. THISTLE [eds.]. 1984. Ecological communities: conceptual issues and the evidence. Princeton Univ. Press, Princeton, New Jersey.

WIENS, J. A. 1977. On competition and variable environments. Am. Sci. 65:590–597.

———. 1981. Single sample surveys of communities: are the revealed patterns real? Am. Nat. 117:90–98.

———. 1986. Spatial scale and temporal variation in studies of shrubsteppe birds. Pp. 154–172 *in* Community ecology (J. Diamond and T. J. Case, eds.). Harper and Row, New York, New York.

——— AND J. T. ROTENBERRY. 1979. Diet niche relationships among North American grassland and shrubsteppe birds. Oecologia 42:253–292.

——— AND ———. 1980. Patterns of morphology and ecology in grassland and shrubsteppe bird populations. Ecol. Monogr. 50:287–308.